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2019-01-10

Laine , A M , Mehtätalo , L , Tolvanen , A , Frolking , S & Tuittila , E-S 2019 , ' Impacts of drainage, restoration and warming on boreal wetland greenhouse gas fluxes ' , The Science of the Total Environment , vol. 647 , pp. 169-181 . https://doi.org/10.1016/j.scitotenv.2018.07.390

http://hdl.handle.net/10138/318101
https://doi.org/10.1016/j.scitotenv.2018.07.390

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Impacts of drainage, restoration and warming on boreal wetland greenhouse gas fluxes

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To be submitted to Science of the total environment as a Primary Research Article

Running head: land use and warming impacts gas fluxes

Abstract

Northern wetlands with organic soil i.e., mires are significant carbon storages. This key ecosystem service may be threatened by anthropogenic activities and climate change, yet we still lack a consensus on how these major changes affects their carbon sink capacities. We studied how forestry drainage and restoration combined with experimental warming, impacts greenhouse gas fluxes of wetlands with peat. We measured CO_2 and CH_4 during two and N_2O fluxes during one growing season using the chamber method.

Gas fluxes were primarily controlled by water table, leaf area and temperature. Land use had a clear impact of on CO_2 exchange. Forestry drainage increased respiration rates and decreased field layer net ecosystem CO_2 uptake (NEE) and leaf area index (LAI), while at restoration sites the flux rates and LAI had recovered to the level of undrained sites. CH_4 emissions were exceptionally low at all sites during our study years due to natural drought, but still somewhat lower at drained compared to undrained sites. Moderate warming triggered an increase in LAI across all land use types. This was accompanied by an increase in cumulative seasonal NEE. Restoration appeared to be an effective tool to return the ecosystem functions of these wetlands as we found no differences in LAI or any gas flux components (PMAX, Reco, NEE, CH_4 or N_2O) between restored and undrained sites. We did not find any signs that moderate warming would compromise the return of the ecosystem functions related to C sequestration.

Keywords: forestry drainage, greenhouse gas, land use, peatland, restoration, open top chamber

1. Introduction

Northern wetlands with organic soil i.e., mires have accumulated a large quantity of peat, accounting for some 30% of global soil carbon (e.g. Yu, 2012). In general, mires have had a small net cooling effect on climate over the Holocene (Frolking, Roulet 2007). Although most undisturbed mires currently act as CO_2 sinks (e.g. Lund et al. 2010) and CH_4 sources (e.g. Lai 2009) to the atmosphere, it is highly uncertain whether mires have a positive or negative feedback in response to global change (Meng et al. 2016). Moreover, this ecosystem function (i.e., carbon sequestration) that mires provide is sensitive to climate variability (Turetsky et al. 2008) and land use change (Ojanen et al., 2013; Renou-Wilson et al. 2014). Utilization of mires for food or timber production usually requires drainage, as the shallow aerobic surface layer of undrained mires is inadequate to support profitable timber or crop growth (Paavilainen, Päivänen 1995). Altogether 30 Mha of non-tropical and 20 Mha of tropical mires have been disturbed by human activities (Joosten 2010), and of this, approximately half has been drained for forestry (Paavilainen, Päivänen 1995; Miettinen et al. 2016). Forestry drainage causes a regime shift from open mires towards forests as it alters the hydrology, increases the aeration of peat and redirects the vegetation succession towards forest species (Laine et al. 1995; Vompersky, Sirin 1997; Mälson et al. 2008). Drainage increases decomposition and therefore CO_2 efflux, while CH_4 emissions usually decrease. In most cases, the increased respiration rates are not exceeded by increased productivity and therefore drained mires functions as C sources and have a climate warming impact (Maljanen et al. 2010; Ojanen et al. 2013; Renou-Wilson et al. 2014; Jauhiainen et al. 2016). There are indicators that some nutrient poor forestry drained mires may continue to act as carbon sinks, however (e.g. Lohila et al. 2011; Ojanen et al. 2013; Hommeltenberg et al. 2014; Ojanen et al. unpublished data). In addition to CO_2 and CH_4, nitrous oxide is a strong potent GHG. Generally, N_2O emissions from pristine mires are low and insignificant, but may increase significantly after drainage, especially with more nutrient rich conditions (Regina et al. 1996; Ojanen et al. 2010; Pearson et al. 2015).

Ecological restoration aims to assist the recovery of an ecosystem that has been degraded, damaged, or destroyed (Hobbs, Cramer 2008) and recent global and national policies (EU Biodiversity Strategy to 2020; Aichi Biodiversity Targets 2011) regard restoration as a crucial means to safeguard biodiversity. Mire restoration has also been promoted as a key climate mitigation tool (e.g. Bonn et al., 2014), and as a means to decrease a country's greenhouse gas (GHG) emissions (IPCC, 2013). At the same time, carbon markets have been identified as possible funding sources for mire restoration schemes (Bonn et al. 2014). However, data on GHG fluxes from restored mires, especially from those restored after drainage for forestry, are very limited.

The principal restoration methods for forestry drained boreal mires are the blocking of ditches to re-create the high water table level, and the removal of excess trees to reduce the transpiration rate and reinstate the landscape typical of natural mires (e.g., Tarvainen et al., 2013). Most research on mire restoration has concentrated on the restoration of peat harvesting areas, which presents quite a different starting point for restoration compared to forestry drainage (Chimner et al. 2017). The few existing studies on C gas fluxes or carbon accumulation rates on restored peat harvesting areas (e.g. Tuittila et al. 1999; Waddington et al. 2010; Strack, Zuback, 2013; Wilson et al. 2016) and forestry drained mires (Komulainen et al. 1998, 1999; Urbanová et al. 2012; Kareksela et al. 2015; Koskinen et al. 2016) indicate that the rising water table increases the rate of field layer photosynthesis, decreases CO_2 efflux and increases CH_4 emissions, thereby partially or fully restoring natural mire functions.

Projected global warming in northern latitudes (IPCC 2013) is going to have its own impact on mire GHG exchange. Experimental warming studies on mires have been carried out with increasing frequency since 2000 (e.g. Wiedermann et al. 2007; Turetsky et al. 2008; Dorrepaal et al. 2009; Chivers et al. 2009; Johnson et al. 2013; Ward et al. 2013; Munir, Strack 2014; Pearson et al. 2015; Peltoniemi et al. 2016; Voigt et al. 2017; Gill et al. 2017; Mäkiranta et al. 2018). These studies, which mostly use open top chambers (OTC's), have shown varied responses of vegetation, microbial communities and gas fluxes to warming within a few years' study periods. In most cases warming has increased respiration, but the impact on photosynthesis and methane emissions has been context dependent and strongly influenced by species composition and water table level: under wet conditions these fluxes may increase, while, under dry conditions and lower water table, in most cases, photosynthesis and methane emissions either decrease or remain unchanged (Turetsky et al. 2008; Dorrepaal et al. 2009; Ward et al. 2013; Munir, Strack 2014; Pearson et al. 2015; Peltoniemi et al. 2016; Gill et al. 2017; Voigt et al. 2017). Denitrification and consequently N_2O fluxes have high temperature sensitivity (Butterbach-Bahl et al. 2013) due to which warming should increase N_2O emissions. This far there have been only a few studies including warming impacts on N_2O emission, and in these, either no changes (Ward et al. 2013, Pearson et al. 2015) or increased emissions (Voigt et al. 2017) have been observed. Further, how warming impacts GHG exchange under different land uses (drainage/restoration) have not been documented in mires thus far.

Our aim is to quantify how forestry drainage and restoration impact GHG dynamics and whether the effects of moderate warming differ between the land uses. To tease out the direct impact of warming we measured CO_2, CH_4 and N_2O fluxes, and leaf area development at six wetlands with peat or primary mires (sensu Joosten et al. 2017) over two growing seasons. Primary mires are successionally young wetlands that, under suitable climatic conditions, will develop into deep peat mires (Tuittila et al. 2013; Joosten et al. 2017) and they are known to rapidly respond to climatic variation (Laitinen et al. 2008; Leppälä et al. 2011a). Four of the sites have experienced long-term water table drawdown due to ditching for forestry in the 1970s, while restoration of two of these sites in 2008 raised water table levels back to the same level as in the two undrained (control) sites (see Laine et al. 2016). Open top chambers (OTC) were used to warm the plots.

We hypothesized that 1) drainage increases CO_2 and N_2O release and decreases CH_4 emissions in comparison to undrained sites. 2) Restoration returns ecosystem functions back to the level of undrained sites rapidly (< 5 years); this means that the restored sites are CO_2 sinks, CH_4 emitters and have very low N_2O emissions. 3) Warming promotes ecosystem respiration but the response of photosynthesis and methane emissions depends on the prevailing hydrology; under undrained and restored conditions warming increases photosynthesis and methane emissions, but under drained conditions these functions remain unchanged. 4) Warming promotes N_2O emissions.

2. Material and methods

2.1. Study area

The study was carried out on the Finnish coast of the Gulf of Bothnia in Siikajoki (drained and restored sites: ~64°48´93N, 24°37´39E; undrained sites: 64°46´91N, 24°38´65E). We selected six primary mires belonging to three land use categories: two undrained (UD1, UD2), two forestry drained in 1970's (D1, D2), and two drained (1970's) sites restored in 2008 (R1, R2). The drainage of site D2 had not resulted in effective regime shift towards forested ecosystem, and the water table was clearly higher than at D1 (see Laine et al. 2016). Restoration was carried out by felling most trees so that ~0–5 trees were left per 100 m^2, and blocking ditches with soil excavated near the ditches. The sites have been formed in the coast following post-glacial land uplift approximately 100-200 years ago (Ekman 1996). They are located 1.5 - 2 m above sea level in small (~0.5-3 ha) depressions between nutrient-poor sand dunes. The organic soil layer laying over sand is only 5-10 cm thick and the organic matter content of the top 10 cm at the undrained sites varies from 25 to 46 %, with pH of 6.3 to 6.6 (Merilä et al. 2006). The sand underneath the organic soil has aeolian origin, it is nutrient poor and has particle size of ~0.17 mm (Hellemaa 1998). The length of growing season in the area is 150 days, the 30-yr average annual temperature 2.6 °C, and the average annual precipitation 541 mm (Revonlahti weather station, Siikajoki, 64° 41′N, 25° 05′E, 48 m a.s.l.; Pirinen et al. 2012; see Table 1 for more climate details).

Based on differences in tree stand and hydrology, the originally drained sites were divided into two groups. Sites D1 and R1 (group 1) had successful drainage results with clearly increased tree growth, while sites D2 and R2 (group 2) had only sparse tree stands. Additionally, the undrained control sites were assigned into these two groups but based on their terrestrial age, so that the younger site (age ~100 yr), UD1, was assigned to group 1 and the slightly older site (age ~150 yr), UD2, to group 2. The undrained sites are open treeless wetlands with the field layer (including small shrubs, herbaceous plants and moss layer) plant community composed of graminoids (*Carex nigra, C. canescens*) and forbs (*Comarum palustre, Equisetum fluviatile, Peucedanum palustre*). The moss layer is composed mainly of

Warnstorfia exannulata and *Calliergon* species, while some patches of *Sphagnum* mosses (e.g. *S. squarrosum, S. fimbriatum*) can also be found. At drained sites, the field layer vegetation is dominated by shrubs (*Vaccinium uliginosum, V. vitis-idaea, Salix repens*) and feather mosses (*Pleurozium shreberii, Polytrichum commune*), although at D2 sedges (*Carex nigra, C. canescens*) are also abundant. The restored sites are open, with only few scattered trees; at the field layer sedges (*Carex nigra, C. canescens*) form the majority of the vegetation and shrubs (e.g. *Salix repens*) are common. Moss layer is sparse and *Warnstorfia exannulata* occurs with remnants of e.g. *Pleurozium schreberi and Polytrichum strictum.* For more details on vegetation composition, see Laine et al. (2016).

At each site, we established ten permanent sample plots and assigned half of them to a warming experiment, covering them with open top chambers (OTC). OTC is a passive warming method that aims at a moderate warming impact of 1-3 °C. The remaining five plots at each site are the ambient temperature (ambient-T) plots. The first set of OTCs was installed in autumn 2008 to sites UD2, D2 and R2 and the second set was installed in spring 2011 to sites UD1, D1 and R1. The OTCs were constructed from durable transparent polycarbonate and had a projected area of 1.5 m^2 (see Pearson et al. 2015). They were removed from the plots during the typical snow-covered period (November-April) to maintain natural snow cover. Soil temperature at 5 and 15 cm depth and air temperature at 30 cm height were monitored continuously within each sample plot at 2h time step during the snow free period (iButton, Maxim Integrated, U.S.). At the beginning of May 2011, a month before the first gas flux measurements, square aluminium collars (58 x 58 cm) were permanently inserted into sample plots to support gas flux measurements. The collar rim reached about 15 cm into the soil, but the deeper roots of trees and vascular plants were left intact. Sample plots were surrounded by boardwalk platforms to avoid trampling.

2.2. Field measurements

We performed weekly to biweekly CO_2 flux measurements from June to November in 2011 and from May to November in 2013, i.e. three and five years after restoration. Monthly methane (CH_4) fluxes were measured from May - September 2011 and June to August 2013. Monthly nitrous oxide (N_2O) fluxes were measured from May to September 2011. Seasonal development of field layer leaf area index (LAI) was monitored during the 2011 and 2013 growing seasons. To facilitate gas flux measurements, the OTC's were lifted up from the warmed plot for the duration of the measurement (15 to 30 minutes).

CO_2 flux was measured with a transparent plastic chamber (60x60x30 cm) that was connected to a portable infrared gas analyser (EGM-4, PP Systems, UK). The chamber was equipped with a fan and a cooling system that maintained the air temperature within 2°C of ambient (Alm et al. 2007). Two to three study sites were measured within the same day, typically between 9 a.m. and 5 p.m. At each sample plot measurements were made under ambient stable light, with the chamber shaded by a mesh fabric to decrease the photosynthetic photon flux density (PPFD) level, and with chamber covered by an opaque shroud (PPFD 0). Each measurement lasted 90-180s. The chamber was lifted and ventilated between measurements to restore the ambient CO_2 concentration. During the measurements, headspace CO_2 concentration, photon flux density (PPFD) and chamber temperature were recorded at 15s intervals.

The net ecosystem CO_2 exchange (NEE) was calculated from the linear change in CO_2 concentration in chamber headspace, as a function of the chamber headspace volume and mean chamber air temperature during the measurement. Dark measurements were used as an estimate of instantaneous ecosystem respiration (Reco). Gross photosynthesis (PG) was calculated by subtracting NEE rate measured in full light and shaded conditions from the subsequent dark measurement (e.g. Alm 2007). Our sign convention shows positive NEE when the ecosystem is a CO_2 sink from the atmosphere.

Methane (CH_4) and **nitrous oxide (N_2O)** fluxes were measured with opaque chambers (60x60x30cm), equipped with fans for air circulation. Four 60 ml gas samples were taken from the chamber with plastic syringes at 5, 15, 25 and 35 minutes after closure. Samples were stored in 12 ml glass vials until analysis. Chamber headspace temperature was monitored during measurements.

Samples from 2011 were analysed for CH_4 and N_2O in the Natural Resources Institute of Finland laboratory at Vantaa, using an Agilent Technologies 7980A gas chromatograph. Samples from 2013 were analysed for CH_4 at the Hyytiälä Forestry Field Station, Finland, using a HP-5890A gas chromatograph. CH_4 and N_2O fluxes were calculated from the linear change in chamber headspace gas concentration as a function of headspace area, volume and mean headspace temperature during the measurement. The correlations (r^2) of the linear change in gas concentrations were generally above 0.9 and 0.8 for CH_4 and N_2O respectively; however, when flux rates were near zero (ranging from -0.05 – +0.03 mg m^{-2} h^{-1}), lower r^2 were typical and these fluxes were not rejected. We rejected only the measurements that where clearly non-linear, without being near zero, altogether 2% of the measurements.

Field layer vascular plant **leaf area index (LAI)** was measured six and seven times during years 2011 and 2013, respectively. Within each sample plot, five 8*8 cm sub-plots were established and the number of leaves of each vascular plant species was counted every three weeks. At the same time leaves of each species were collected outside the gas flux plots, carefully mounted on paper and scanned. Leaf area was digitally analysed from the images. We calculated LAI of each species as a product of the number of leaves and the average leaf size. Seasonal LAI development was estimated with statistical modelling, see section 2.4.1.

Supporting measurements of soil temperature and water table level were made during gas flux campaigns. During flux measurements, we manually measured soil temperature at 5, 10 and 15 cm depth next to each sample plot and measured water table level using perforated pipes that were inserted into the soil at close vicinity of the sample plots. Soil or moss surface was used as the zero reference level.

2.3. Carbon sequestration of the tree stand

Tree stand characteristics were measured in 2005, 2009 and 2013 at 12 and 14 permanent circular plots at sites all sites. The number of all trees taller than 1.3 m and diameter at breast height (D_{bh}) more than 45 mm was counted and D_{bh} of all trees was measured. For each species we chose the tree with largest D_{bh} and at least one tree from diameter classes 10 - 20 cm and 4.5 – 10 cm as sample trees. From these sample trees height (h) and living crown length and width were measured. Based on these data we calculated the stand density (trees ha^{-1}) and annual volume increment with the KPL software (Heinonen, 1994).

While the tree stand of undrained and restored sites was either absent or minor, at drained sites the carbon sequestration of the tree stand was estimated as follows: To calculate the above- and belowground biomass for birches and pines separately, we used species-specific models developed by Repola, (2008; 2009). Above ground biomass estimates were based on D_{bh} and tree height, while the below ground biomass estimates were based on D_{bh}. The tree stand biomass difference between years 2013 and 2005 was used to calculate the annual biomass increment and converted it to carbon using the frequently applied conversion factor 0.50 (see e.g. Laiho, Laine 1997).

2.4. Data analysis

We applied linear and nonlinear hierarchical mixed-effects modelling to quantify how long-term drainage, restoration and moderate warming impact LAI development and GHG flux dynamics of the field layer of the primary mires. We used two steps in the gas flux modelling. First, we related gas flux parameters (e.g. PMAX and Reco, see Eq. 4 below) to so-called stable factors, namely land use category, warming treatment, year and site group (group 1: UD1, D1 and R1; group 2: UD2, D2 and R2). Then we built so-called "full models" that also included environmental variables (temperature, LAI etc.) as explanatory variables of the gas flux parameters. The model building was based on known properties of the natural process, where the effects of treatments and environmental factors on the model parameters were concurrently analysed and added sequentially to the model in order of importance. The prediction of the LAI model is included as an environmental variable in the CO_2 and CH_4 models.

2.4.1. LAI modelling

Seasonal LAI development can be described with a log-normal unimodal function with parameters for maximum leaf area ($LMAX_{ijk}$) and timing of maximum leaf area ($DMAX_{ijk}$). Our modelling procedure follows that presented by Mäkiranta et al. (2017).

$$y_{ijkl} = LMAX_{ijk} \times exp\left[-0.5\left(\frac{log\left(\frac{T_{ijkl}}{DMAX_{ijk}}\right)}{G_{ijk}}\right)^2\right] + e_{ijk};\ LMAX_{ijk}, DMAX_{ijk}, G_{ijk} > 0 \quad (1)$$

where y_{ijkl} is the observed LAI ($m^2\ m^{-2}$) at light level l within year k within plot j within site i, and the predictor T_{ijkl} is the corresponding Julian days since the beginning of year. The parameters of the model are the maximum LAI ($LMAX_{ijk}$), its timing ($DMAX_{ijk}$), and the scale parameter G_{ijk}, which is related to the temporal scale of LAI development. The residuals (e_{ijk}) did not show signs of inconstant variability and temporal autocorrelation, and it was therefore assumed that they are independent with zero mean and common variance (σ^2). To quantify the impacts of treatments on the LAI parameters, they were further written as linear functions of fixed predictors (land use, warming, year and site group) and three nested random effects for site, plot within site, and year within plot within site. Logarithmic form was used to ensure positive values of parameters in all cases. The resulting submodels are:

$$LMAX_{ijk} = \exp(\boldsymbol{\beta}^{\boldsymbol{LMAX}}{}'\boldsymbol{x}_{\boldsymbol{ijk}}^{\boldsymbol{LMAX}} + a_i^{LMAX} + b_{ij}^{LMAX} + c_{ijk}^{LMAX}) \quad (2)$$

$$DMAX_{ijk} = \exp(\boldsymbol{\beta}^{\boldsymbol{DMAX}}{}'\boldsymbol{x}_{\boldsymbol{ijk}}^{\boldsymbol{DMAX}} + a_i^{DMAX} + b_{ij}^{DMAX} + c_{ijk}^{DMAX}) \quad (3)$$

$$G_{ijk} = \exp(\boldsymbol{\beta}^{\boldsymbol{G}}{}'\boldsymbol{x}_{\boldsymbol{ijk}}^{\boldsymbol{G}} + a_i^{G} + b_{ij}^{G} + c_{ijk}^{G}) \quad (4)$$

where the inner product $\boldsymbol{\beta}^{LMAX\,\prime}\boldsymbol{x}_{ijk}^{LMAX}$, $\boldsymbol{\beta}^{DMAX\,\prime}\boldsymbol{x}_{ijk}{}^{DMAX}$ and $\boldsymbol{\beta}^{G\,\prime}\boldsymbol{x}_{ijk}{}^{G}$ include the fixed effects of the treatments on LMAX and DMAX (the terms included in the final models will be shown in result tables). The normally distributed random effects for different parameters at the same level (e.g. a_i^{LMAX}, a_i^{DMAX}, a_i^{G}) were assumed to be uncorrelated to achieve convergence (Pinheiro and Bates 2000). They modelled the variability that was not explained by the fixed effects, and simultaneously the dependence due to grouping in the data. Submodels (2 and 3) were included in Equation 1 and the resulting model was fitted in one step. We used approximate conditional F- tests (Pinheiro, Bates 2000) and Akaike information criterion (AIC) in model selection. Models were fitted using the nlme package of R (R Core Team 2016), following Pinheiro and Bates (2000). To facilitate CH_4 flux modelling, we also used the same method to model the LAI of species with aerenchyma (mainly sedges in our sites) (LAI_S). See Supporting information 1 for model details.

2.4.2. CO_2 flux modelling

To determine the effects of land use and warming on the light response parameters of photosynthesis, and their dependences to environmental factors (LAI, air temperature, soil temperature) we applied a nonlinear mixed-effects model with the hyperbolic light saturation curve (e.g. Lappi, Oker-Blom 1992):

$$A_{ijklm} = R_{ecoijkl} + \frac{PMAX_{ijkl}PPFD_{ijklm}}{\alpha_{ijkl}+PPFD_{ijklm}} + e_{ijklm} \qquad (4)$$

where the response A_{ijklm} is the observed NEE (mg m^{-2} h^{-1}), and the predictor $PPFD_{ijklm}$ is the photosynthetic photon flux density (µmol m^{-2} s^{-1}) on measurement *m* of day *l* of year *k* of plot *j* at site *i*. The parameters to be estimated are respiration ($Reco_{ijkl}$), photosynthetic capacity i.e. the maximum rate of light-saturated gross photosynthesis ($PMAX_{ijkl}$) and the maximum quantum yield of CO_2 assimilation (α_{ijkl}), i.e., light use efficiency at low light. The residual (e_{ijklm}) is normally distributed with mean zero and constant variance. Parameters $PMAX_{ijkl,}$

$Reco_{ijkl}$ and α_{ijkl} were written as linear functions of fixed predictors and random effects. These submodels are:

$$PMAX_{ijkl} = \exp(\boldsymbol{\beta}^{\boldsymbol{PMAX}}{}'\boldsymbol{x}_{\boldsymbol{ijkl}}^{\boldsymbol{PMAX}} + a_i^{PMAX} + b_{ij}^{PMAX} + c_{ijk}^{PMAX} + d_{ijkl}^{PMAX}) \quad (5)$$

$$Reco_{ijkl} = \exp(\boldsymbol{\beta}^{\boldsymbol{R}}{}'\boldsymbol{x}_{\boldsymbol{ijkl}}^{\boldsymbol{R}} + a_i^{R} + b_{ij}^{R} + c_{ijk}^{R} + d_{ijkl}^{R}) \quad (6)$$

$$\alpha_{ijkl} = \exp(\boldsymbol{\beta}^{\boldsymbol{\alpha}}{}'\boldsymbol{x}_{\boldsymbol{ijkl}}^{\boldsymbol{\alpha}} + a_i^{\alpha} + b_{ij}^{\alpha} + c_{ijk}^{\alpha} + d_{ijkl}^{\alpha}) \quad (7)$$

The random effects ($a_i^{PMAX} + b_{ij}^{PMAX}, \ldots, c_{ijk}^{\alpha} + d_{ijkl}^{\alpha}$) were assumed to have mean zero and common variance; the effects for different parameters at the same level were assumed to be uncorrelated. In practice, the model building started with a model without predictors and with random effects d_{ijkl} only. The predictor that showed strongest relationship with the random effects was thereafter included in the fixed part using appropriate transformation and the model was re-estimated. The random effects of the updated model were extracted and their relationship was again explored against the current and potential new predictors. These steps were iterated until the random effects did not show any unexplained trends. The final model was then fitted using the above-specified full random effect structure and the fixed effects were tested using conditional approximate F- tests on the fixed effects ($p > 0.05$). The number of replicates in our data is small, and therefore the effects of land use or warming needs to be very large to become statistically significant. To maximally utilize our data and provide essential information for future research efforts, we therefore report parameter estimates from the full model and their confidence intervals regardless of their p-values, as in Mäkiranta et al. (2017).

To separate the impacts of land use category and warming treatments from those of environmental variables, we used two sets of fixed predictors (e.g. $\boldsymbol{\beta}^{\boldsymbol{PMAX}}{}'\boldsymbol{x}_{\boldsymbol{ijkl}}^{\boldsymbol{PMAX}}$) in the sub-models (eq. 5-7). The first set included only categorical treatment effects, while the second set also included environmental variables. For the first set, the categorical predictors were land use, warming, measurement year and site group. For the second set, the following environmental variables and their transformations were included to form the full model of $PMAX_{ijkl}$: LAI was included as transformation LAI2=ln(1-exp(-LAI)) to take into account the self-shading of leaves through Beer-Lambert's law (Wilson 1959). Air temperature was included using a three-knot spline, with knots placed at 15°C, 20°C and 25°C (Harrell 2001), which allowed an optimum temperature within the range of observations (0 – 37°C). The full model of R_{ijkl} included the predicted plot-specific LAI from model (1) in logarithmic form, i.e., respiration was assumed to be linearly related to LAI. Air temperature was used in linear form, which implies an exponential response of respiration to temperature. In addition to air temperature, 15-cm soil temperature was included in the R_{ijkl} models in form with a minimum at 10°C, which allows exponential response to soil temperatures below 10°C. For the submodel of parameter α_{ijkl} (eq. 7), only land use category was used as a fixed predictor. The chosen transformations provided better fits to the data than non-transformed or logarithmically transformed predictors, and satisfactorily modelled all clear trends from the random effects. See Supporting information 2 for model details.

2.4.3. CH_4 and N_2O flux modelling:

We used linear mixed-effects models to analyze the effects of land use and warming on CH_4 and N_2O fluxes, and their dependences on environmental variables. Inverse transformation, $1/(CH_4+0.3)$, was used for CH_4 to homogenize the residual variance of the model (Appendix 3). Similar to CO_2 modelling, in the first CH_4 and N_2O modelling steps we included categorical treatment effects as fixed predictors. These were land use category, warming, their interaction, *y*ear and site group. In the second step, we formed the full model that also includes environmental variables. For CH_4 flux, the full model included sedge LAI (LAI_S), air temperature (Ta), soil temperature at 5 cm (T5) and water table depth (WT), which was included using a three-knot spline, with knots placed at values -55, -40 and -25 cm (Harrell 2001), which allowed an optimum water table within the range of observations (-80 cm – 0 cm). For N_2O flux, the full model included total LAI, WT, Ta and T5. Random intercepts were assumed for levels site and plot and measurement time. The plots were nested within sites and crossed with measurement time. See Supporting information 3 and 4 for model details.

2.5. Reconstructing seasonal cumulative gas fluxes

We used the fixed part of the full models of CO_2 (eq. 4-7) and CH_4, described earlier, to estimate the seasonal cumulative fluxes of NEE and CH_4. Reconstructions were made with hourly time step and results are reported per square meter. The environmental data for reconstructions was attained as follows: hourly values of PPFD from the Siikajoki, Ruukki weather station (64°68′N, 25°09′E, Finnish Meteorological Institute). PPFD under the forest canopy in site D1 was estimated as in Badorek et al. (2011). Tree canopy leaf area (CLAI) for the calculations was estimated using the biomass equations of Repola (2008, 2009) for Scots pine and birch, and the specific leaf areas of 11 $m^2\ kg^{-1}$ DW for pine (Luoma 1997), and 25 $m^2\ kg^{-1}$ DW for birch (Parviainen 1999). Soil temperature at 5 and 15 cm depth and air temperature at 30 cm height were continuously recorded beside each sample plot at 2h time step (iButton, Maxim Integrated, U.S.) and interpolated to hourly values, and averages of warmed and ambient-T plots were calculated for each site. Water table was measured during gas flux campaigns, on average once per week. This data was linearly interpolated into hourly values and site averages were calculated. Hourly LAI was predicted using the fixed part of the LAI model for warming and ambient-T plots of each site.

We reconstructed fluxes for 1 May to 30 September. We had continuous environmental data from 10 May to 30 September for 2011 and from 14 May to 30 September for 2013. For the beginning of May, we multiplied the average May flux rate by the number of missing hours. We acknowledge that gas exchange occurs also during time period not included here. As N_2O flux rates per site were rather constant and not explained by any environmental variable, we estimated the seasonal cumulative flux by multiplying the average flux rate by the number of hours during 1 May to 30 September.

Global warming potentials (GWP)

In order to compare the GHG balance of the different land uses, we calculated the GWP's for each site for growing seasons 2011 and 2013, based on a 100-year time horizon. We used the cumulative seasonal NEE, CH_4 and N_2O fluxes calculated per site and included the carbon sequestration of the tree stand in the NEE of drained sites by adding the estimated annual CO_2 sequestration. GWP's were not calculated for the warming treatment plots as those would not include the response of tree stand to warming. In addition, the N_2O flux estimates from season 2011 were used for 2013. The cumulative seasonal CO_2, CH_4 and N_2O flux estimates were multiplied by 1, 28 and 265, respectively to convert all to CO_2-equivalent fluxes that can be summed (Myhre et al 2013). Negative GWP values indicate a net cooling effect on the climate and positive values indicate a net warming effect.

3. Results

3.1. Environmental conditions

The average WT in the undrained sites was -8 and -27 cm, in the restored sites -11 and -24 cm, and in the drained sites -28 and -41 cm during years 2011 and 2013, respectively, (negative values indicate belowground WT). The two drained sites differed from each other, so that D2 had shallower WT than D1 in both years (Fig. 1). During late summer 2013 all sites experienced very low WT for an extended period (Fig. 1b).

Open top chambers (OTC) increased average air temperatures by 1.4°C compared to ambient-T plots. The difference between OTC and Ambient-T plots was higher during spring (1.8°C) and summer (1.6°C) than during autumn (0.5°C) (Table 1). Average soil temperatures were not elevated by the OTCs (Table 1). Annual and summer average temperatures were higher, and precipitation slightly higher, in years 2011 and 2013 than the long term averages (Table 2).

3.2.Leaf area index

Land use had a clear impact on LMAX as it was lower in drained sites and at the comparable level in restored and undrained sites (Fig. 2, Table S1.1.). Warming treatment increased LMAX on average by 0.4 m^2m^{-2}, and LMAX was lower in year 2013 than in 2011 (Fig.2, Table S1.2.). The timing of the LMAX (LMAX_T) was dependent on land use and year (Table S1.1.). LMAX was attained earlier in restored sites than in undrained sites and earlier in year 2013 than in 2011 (Table S1.2.). The site groups 1 and 2 did not differ from each other (Table S1.2.)

3.3. Greenhouse Gas exchange

3.3.1. CO_2 exchange

At the ambient-T plots, average field layer gross photosynthesis at full light (PPFD>800) ranged from 537 to 1116 mg CO_2 m^{-2} h^{-1}. In the warmed plots, the range was from 657 to 1122 mg CO_2 m^{-2} h^{-1}. (Table 3). Average ecosystem respiration rates (Reco) ranged from 337 to 751 mg CO_2 m^{-2} h^{-1}. In the warmed plots, the range was from 335 to 525 mg CO_2 m^{-2} h^{-1} (Table 3).

We based our CO_2 modelling on the relationship between NEE and PPFD, which is a strong controller of photosynthesis (Fig. 3). The nonlinear mixed effect models showed that P_{MAX} varied between land use categories; drained sites had lower P_{MAX} than undrained sites (Table S2.2.). Experimental warming, as such, had no impact on P_{MAX}. (Table S2.1.) After inclusion of environmental variables (i.e. the full model), the effect of land use was overridden by air temperature and LAI implying that the treatment impact is dominated by changes in these factors (Table S2.3. and S2.4.). The model indicated that drained sites had slightly higher Reco than undrained sites, (Table S2.2.). As the site group, i.e. group 1 with successful drainage and group 2 with low drainage impact, was significant in the model, so that group 1 had higher Reco, the difference between properly drained site D1 and undrained sites is stronger than indicated by the insignificant p-value (Table S2.2.). At the drained sites, the respiration component includes tree root respiration but not respiration of the above-ground parts of the trees, therefore the real Reco would be higher. The tree stand net primary productivity is included in the estimate of seasonal NEE. Warming had no impact on Reco, and Reco was higher in year 2013 than in 2011. In the full model, the environmental variables air and soil temperature and LAI had a significant impact on Reco (Table S2.3., Table S2.4.). The maximum quantum yield of CO_2 assimilation (α), i.e., the light-use efficiency at low light, was lower at drained sites and similar in restored and undrained sites (Table S2.2., Table S2.4.).

The growing season cumulative NEE of the field layer and soil varied between -1088 (source) and +567 (sink) g CO_2 m^{-2} $season^{-1}$. Unlike in undrained and restored sites, in the drained sites the tree stand also sequestered carbon. The tree stand volumes were low, being 106 and 37 m^3 ha^{-1} in sites D1 and D2, respectively at year 2013. The average annual volume increment since 2005 has been 5 and 2 m^3 $ha^{-1}year^{-1}$ representing annual carbon sequestration of 959 and 423 g CO_2 m^{-2} for sites D1 and D2, respectively. As most of the carbon sequestration to the trees occurs during the growing season, we consider the annual value comparable to our growing season field layer NEE estimate. At the more productive site, D1, the NEE after inclusion of tree stand sequestration was about the same magnitude as in undrained site, while site D2 was a strong CO_2 source (Fig. 4a). Generally, all the sites varied from being small sources or sinks with clear inter annual variation. NEE was lower/negative during dry year 2013 and higher under warming treatment than under ambient-T conditions (Fig. 4a).

3.3.2. Methane emissions

The average measured CH_4 emissions varied between land use and warming treatments from 0.21 to 1.00 mg CH_4 m^{-2} h^{-1} (Table 3). The monthly variation in flux rates was rather large, with highest fluxes in early summer and lower fluxes in late summer and autumn (Fig. 5). Drained sites had somewhat lower emissions than undrained ones. Experimental warming increased CH_4 flux in undrained sites, but not in restored and drained sites (Table S3.1, Table S3.2.). When environmental variables were included in the model, the variation in CH_4 flux was explained by water table and air temperature (Fig. 6, Table S3.3.), leaving LAI with insignificant effect. Seasonal CH_4 emissions were lowest at drained sites (on average 0.2 g CH_4 m^{-2} $season^{-1}$) and highest at restored sites (on average 1.5 g CH_4 m^{-2} $season^{-1}$) (Fig 4b).

3.3.3. N_2O emissions

The average measured N_2O emissions varied between treatments from 0.15 to 0.27 mg m^{-2} h^{-1} (Fig. 7, Table 3). Drained sites had higher emissions than undrained sites and warming caused a slight but statistically insignificant increase on the emission, however, less in drained sites than in other sites (Table S4.2.). None of the environmental variables included in the model (WT, Ta, LAI) explained the variation in flux rates (Table S4.3.). The seasonal N_2O emissions were lowest at undrained sites (on average 0.6 g N_2O m^{-2} $season^{-1}$) and highest at drained sites (on average 0.9 g N_2O m^{-2} $season^{-1}$) (Fig 4c).

3.3.4. Global warming potential

At ambient-T conditions the GWP (CO_2 equivalent emissions) was positive, i.e., warming, at most sites, and the drier year 2013 had higher GWP than 2011 (Table 4). The carbon sequestration of tree stand at site D1 clearly decreased its GWP.

4. Discussion

Our experimental set-up with two references, namely the forestry drained starting point and the undrained goal, allows the examination of a restoration pathway – is it going towards the pristine conditions or to some new state? Our results show that restoration had led towards pristine conditions by returning, within 3 years, the key ecosystem functions typical of pristine mires. We found no differences in LAI or any gas flux components (PMAX, Reco, NEE, CH_4 or N_2O) between restored and undrained sites, while the long-term forestry drainage had changed all these ecosystem functions. The response of the functions to restoration had same direction but was faster than what was observed from deep peat *Sphagnum* mires also drained for forestry (Kareksela et al. 2015).

4.1. Field layer leaf area index

At the forestry-drained state, which is the starting point for restoration, the LAI of field layer vegetation was lower than at undrained state. This difference was mostly caused by a decrease of sedge cover greater than the increase of shrub cover, indicating secondary succession towards forest vegetation (the changes in species composition are shown at Laine et al. 2016). During secondary succession following drainage, the closing tree canopy increases the competition for light and decreases the biomass of field layer vegetation, especially in minerotrophic mires (Laine et al. 1995; Minkkinen et al. 1999). In our study, no longer than three years after restoration, LAI had already reached the range of undrained sites and vegetation composition was shifting towards that of undrained sites (Laine et al. 2016). We conclude that the largest share of the LAI change was due an increase in sedge cover (Laine et al. 2016). Sedges are known to be the first species to respond to increased water table level and light (Komulainen et al. 1999; Tuittila et al. 2000b; Graf et al. 2008).

OTC's installed at mires generally have rather modest impact on temperatures, with air temperature increasing typically less than 2°C and soil temperatures less than 1°C (Turetsky et al. 2008; Chivers et al. 2009; Johnson et al 2013; Munir, Strack 2014; Pearson et al. 2015; Buttler et al 2015). Similarly, OTC's in our young primary mires increased the air temperature less than 2°C, while soil temperature remained similar to the ambient-T plots. The most evident effect of warming was the increased field layer LAI, which was observed in all land use categories. This is in contrast to the study by Mäkiranta et al. (2017), who observed no warming-induced changes in total leaf area in two sedge fens. The fast responses of vascular plant LAI to warming at our sites may be due to the insignificant cover of

Sphagnum mosses, which are known to buffer plant community responses to environmental manipulations (Wiedermann et al. 2007). Warming with OTCs has been shown to increase vegetation height (Cornelius et al. 2014) and Normalized Difference Vegetation Index (NDVI) (Buttler et al 2015), but the impacts on vegetation cover have been highly species-specific (Buttler et al 2015). As an example, dwarf shrubs and graminoids have showed a greater growth response to warming than herbaceous perennials (Kudernatsch et al., 2008). On the other hand, we observed increased LAI under all land use types despite their differences in plant community composition. According to a meta-analysis by Elmendorf et al. (2012), in tundra there is large heterogeneity in the direction and magnitude of vegetation responses, depending for example on the duration of warming experiment, ambient summer temperatures, and moisture status.

Differences in LAI between the two measurement years of our study highlight the responsiveness of primary mires to short-term water table drops. The summer 2013 drought caused a clear decrease in LAI across the land use categories, despite similar average temperatures to summer 2011.

4.2. CO_2 exchange

We found very high interannual and between site variability in the NEE of undrained sites (ranging from -300 to 300 g CO_2 m^{-2} $season^{-1}$). Such interannual variation is a typical phenomenon in mires, and extreme drought can switch a mire into a CO_2 source (e.g. Alm et al. 1999, Lund et al. 2012). When considering the wintertime CO_2 emission of ~130 g CO_2 m^{-2} $season^{-1}$ (estimated for the undrained sites at winter 2003/2004 by Leppälä et al. 2011b), the annual uptake during year 2011 fits well within the range measured from temperate and boreal mires (Roulet et al., 2007; Aurela et al. 2009; Christensen et al. 2012; McVeigh et al. 2014; Peichl et al. 2014; Helfter et al. 2015), while during 2013 the NEE was clearly lower.

Higher soil respiration rates are considered the main consequence of mire drainage, as decomposition in well-aerated soil is many-fold more efficient than in anoxic conditions and root respiration increases along with developing tree stands (e.g. Silvola et al. 1996; Minkkinen et al. 2007; Maljanen et al. 2010; Chivers et al. 2017). In accordance, we observed higher ecosystem respiration (excluding aboveground tree respiration) from the drained sites, particularly from the successfully drained site D1 compared to undrained ones. In addition to lower water table, the sites differ from each other in that drained sites have significant amount of tree roots, which are lacking from undrained sites. Based on estimate from a Finnish forestry drained mire, 10 to 20 % of the respiration may be produced by tree roots (Minkkinen et al. 2018). In addition to increased respiration rates, drainage decreased the photosynthetic capacity (PMAX) of the field layer vegetation and shifted production to the growing tree stand. The low PMAX of field layer vegetation results from a combination of 1) lower LAI, which is a proxy of the amount of photosynthetic tissue and therefore sets the limit for photosynthesis (e.g. Barr et al. 2004; Wilson et al. 2007), and 2) the different species composition due to differences in species photosynthetic capacities (e.g. Laine et al. 2016; Korrensalo et al. 2016). When combined with lower light levels under the tree canopy, the cumulative growing season NEE of field layer was clearly lower at the drained sites than at the undrained sites, and was similar to a drained deep peat pine bog in Southern Finland (Badorek et al. 2011). Including tree stand C sequestration, the well drained site D1 turned into a small CO_2 sink during the less dry year, while the site D2 was a strong CO_2 source during both years. In some forestry drained mires, the growth of the tree stand has exceeded the C release from the decomposing peat, resulting in a large C sink (e.g. Lohila et al. 2011; Ojanen et al. 2013; Hommeltenberg et al. 2014; Minkkinen et al. 2018; Ojanen et al. unpublished data,). All such sites have been nutrient poor but still able to support intensive tree growth. The tree growth in our site D2, on the other hand, was low due to poor drainage and regular spring and autumn floods (Laine et al. 2016); this led to high CO_2 emissions.

Unlike in the drained sites, we did not find any differences in PMAX, Reco and NEE between restored and undrained sites. Indeed, decreased respiration rates are an expected phenomena and a major goal of rewetting in mires (e.g. Waddington et al. 2010; Knox et al. 2015; Wilson et al. 2016).

In contrast to our hypothesis, experimental warming increased NEE, i.e. CO_2 sink capacity in all land use types. The magnitude of the warming impact was, however, secondary to that of land use induced water table alteration. Biochemical processes linked with photosynthesis are controlled by temperature (e.g. Medlyn et al. 2002) and the importance of temperature in controlling respiration in mires has been well documented (e.g. Lafleur et al. 2005; Mäkiranta et al. 2009). Correspondingly, we found that both components of CO_2 exchange, PMAX and Reco, were dependent on air temperature. However, the impact of warming was seen only after the instantaneous measured flux rates were reconstructed to cumulative growing season fluxes. As OTC's were lifted up during the instantaneous measurements, they are made under ambient temperature conditions, which are similar at both OTC and ambient-T plots and not influenced by the OTC warming except via the indirect effect of increased leaf area. In several other studies moderate warming has had very small or no impact on CO_2 fluxes (Chivers et al. 2009; Johnson et al. 2013; Pearson et al. 2015), while some have reported a moderate increase in respiration (Ward et al. 2013). Voigt et al. (2017) observed clear decrease in NEE, as, in addition to increased ecosystem respiration, plants were suffering from increased water deficient due to warming. Ward et al. (2013) noticed that the response was dependent on the existing plant groups so that NEE increased only when graminoids were removed, leaving only shrubs and mosses. In our sites, plants seemed to be able to respond to warming by increasing leaf area and photosynthesis and we observed quite similar increases in cumulative NEE due to warming in shrub-dominated drained sites and graminoid-dominated undrained and restored sites.

4.3.Methane emissions

Methane emissions were at the low end of those measured from different fens (e.g. Suyker et al. 1996; Rinne et al. 2007; Nilsson et al. 2008; Leppälä et al. 2011c; Trudeau et al. 2013). Similar to previous findings, CH_4 emissions were controlled by water table and air temperature (e.g. Moore, Dalva 1993; Bubier et al. 1993; Pelletier et al. 2007; Lai 2009). Water table and air temperature overruled any effects of LAI in explaining the CH_4 emissions, even though vegetation functions as a supply of organic material for methanogens and as a pathway of methane through the aerobic peat layer (Ström et al. 2003; Garnet et al. 2005).

While the literature shows that drainage decreases or ceases CH_4 emissions (Martikainen et al. 1995; Roulet, Moore 1995; Maljanen et al. 2010; Frolking et al. 2011), we found only slightly lower CH_4 emissions from drained sites compared to undrained ones. This small difference is likely a result of the low water table throughout most of the studied growing seasons at all sites. When comparing our measurements with previous study from the same undrained sites it is evident that the low water table had decreased the CH_4 fluxes: during a wet year (2004), the seasonal cumulative CH_4 emission was much higher than during our measurement years (8.8 compared to 0.8 g CH_4 m^{-2} $season^{-1}$; Fig. 4b, Leppälä et al. 2011c). Mire restoration is often associated with highly increased methane emission, although there is a large range of emissions (0-91 g CH_4 m^{-2} yr^{-1}) between the studies, caused by differences in water table, vegetation composition and time since restoration (Knox et al. 2014; Nahlik, Mitsch, 2010; Hendriks et al. 2007; Herbst et al., 2013; Wilson et al. 2016). We assume that during wetter years CH_4 emissions at the restored sites would be similar to those that have been measured from these undrained sites (Leppälä et al 2011c). This is supported by similarities in the vegetation composition and WT dynamics between our undrained and restored sites. In addition, there are indications that at our sites the soil microbial community, both methanogens and methanotrophs, was recovering rapidly after restoration (Putkinen et al. 2012).

Warming increased CH_4 fluxes, but only at the undrained sites. Both microbial methane production and oxidation are dependent on temperature (Dunfield et al. 1993), and the existing studies on warming impacts are inconclusive. Turetsky et al. (2008) found increased and Peltoniemi et al. (2016) decreased methane emissions in fens, while some other studies have found no impact (Johnson et al. 2013; Pearson et al. 2015). The warming impact is likely dependent on moisture conditions as in water-saturated conditions emissions have increased, while the opposite has been observed from drier hummocks (Munir, Strack 2014; Gill et al. 2017). This is partly in accordance with our study, as the water table was generally higher in undrained than in drained sites. Why CH_4 fluxes at the restored sites did not respond similarly to warming remains an unanswered question, however, as the restored and undrained water tables were similar, and Putkinen et al. (2012) showed that the methanogen community was not poorly developed and therefore would be able to respond to warming.

4.4. Nitrous oxide

Nitrous oxide plays a minor role in the GHG dynamics of these primary mires. We measured higher N_2O fluxes from drained sites than from undrained sites, which is typical especially in fen mires (Regina et al. 1996; Ojanen et al. 2010; Pearson et al. 2015). The flux rates were within the range measured from other Finnish forestry drained mires (Ojanen et al. 2010). We observed modest seasonal variability in the flux rates and were not able to explain the fluxes with environmental variables, although temperate and moisture conditions are generally seen as regulators of seasonal flux variability (Kitzler et al. 2006). The experimental warming seemed to increase the N_2O fluxes, likely due to high temperature sensitivity of denitrification and consequently N_2O fluxes (Butterbach-Bahl et al. 2013). Our finding is in contrast to earlier studies from pristine mires (Ward et al. 2013, Pearson et al. 2015), but the disparity may be explained by differences in moisture conditions and other site characteristics as they may restrain the stimulating effect of temperature (Butterbach-Bahl, Dannenmann 2011). Our data set on N_2O is however, limited to five measurement campaigns, and do to a sporadic nature of N_2O emissions (Butterbach-Bahl et al. 2013) we would not draw any strong conclusions from this result.

5. Conclusions

In our study, restoration appeared to be an effective climate mitigation tool; restoration quickly returned the ecosystem functions of undrained primary mires and reversed unwanted impacts of drainage, such as high respiration rates. The global warming potential (GWP) varied largely between sites and years, and most sites, including the undrained ones, had a positive GWP, especially during the dry year 2013. It seems that restoration of boreal forestry drained mires is relatively fast and easy task compared to mires drained for agricultural purposes (Klimkowska et al. 2007) or peat harvesting areas (Chimner at al. 2017). A likely reason is that forestry drainage causes less disturbance to vegetation cover and soil. These differences should be further evaluated. In restored, as well as other sites, warming accelerated net ecosystem CO_2 sink function, due to increased LAI and we did not see any signs that moderate warming would compromise the climate mitigation of restoration.

Acknowledgements

We acknowledge funding from the University of Helsinki and Kone foundation (A. M. Laine), the Natural Resources Institute Finland (A. Tolvanen), the Fulbright-Finland and Saastamoinen Foundations (S. Frolking), and the Academy of Finland (project code 287039) (E.-S. Tuittila). We thank Ivka Vasil`ka, Annukka Närhi and Mirkka Kotiaho for field assistance.

Data Statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Supplementary material for online publication:

Supporting information 1. Nonlinear mixed-effect model based on leaf area index

Supporting information 2. Nonlinear mixed-effect model based on CO_2 flux measurements

Supporting information 3. Linear mixed effect models based on CH_4 measurements

Supporting information 4. Linear mixed effect models based on N_2O measurements

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Table 1. Average air and soil temperature (°C) at OTC warming plots and ambient-T plots in Undrained, Restored and Drained land use category during spring (May), summer (June-August) and autumn (September-November). Statistically significant ($p<0.05$) differences between OTC and Ambient-T plots are marked with * (ANOVA-tests).

		Spring		Summer		Autumn	
		OTC	Ambient-T	OTC	Ambient-T	OTC	Ambient-T
Air T at 15cm	Undrained	18.9	16.8*	17.1	15.8*	7.4	6.5*
	Restored	18.7	17.7	17.0	16.3*	7.8	7.1*
	Drained	17.0	16.3	15.9	15.3	7.3	6.9
Soil T at 5cm	Undrained	11.4	11.4	14.9	14.6	9.1	8.3
	Restored	11.5	10.8	12.5	12.7	9.4	9.7
	Drained	8.3	8.2	12.5	12.7	8.7	8.5

Table 2. Average annual and summer time temperature (T) and precipitation (Prec) in study years 2011 and 2013, and the long-term averages for period 1981-2010. Summer denotes for June-August. Data from Siikajoki, Revonlahti weather station, Finnish Meteorological Institute and from Pirinen et al. 2012.

Period	T year, °C	T summer, °C	Prec year, mm	Prec summer, mm
2011	4.3	16.0	570	203
2013	4.2	15.4	585	220
30 yr average	2.6	14.2	541	199

Table 3. Mean measured CO_2, CH_4 and N_2O fluxes under different land use and warming treatments. UD = undrained, R = restored, D = drained, A = ambient-T, O = OTC warming, PG = gross photosynthesis Reco = ecosystem respiration, and NEE = net CO_2 exchange. Unit for gas fluxes is mg $CO_2/CH_4/N_2O$ m^{-2} h^{-1}. The mean for PG and NEE is based only on light saturated measurements with PPFD > 800 µmol m^{-2} s^{-1}.

Year	Land use	Warming	PG @PPFD>800	Reco	NEE @PPFD>800	CH_4	N_2O
All	UD1	A	955	396	496	0.2	
		O	1041	380	594	0.7	
	UD2	A	1115	414	605	0.7	
		O	935	374	490	1.1	
	R1	A	1116	409	517	1.1	
		O	1122	364	613	1.4	
	R2	A	959	374	446	0.6	
		O	919	335	469	0.6	
	D1	A	537	751	-74	0.0	
		O	657	525	141	0.1	
	D2	A	796	337	349	0.4	
		O	830	363	365	0.4	
2011	UD1	A	990	335	591	0.2	0.1
		O	1135	332	756	0.8	0.2
	UD2	A	983	313	609	0.6	0.2
		O	797	317	459	1.3	0.2

	R1	A	826	361	221	1.4	0.2
		O	873	327	417	1.8	0.3
	R2	A	994	363	522	0.8	0.2
		O	995	316	569	0.9	0.3
	D1	A	549	692	-40	0.0	0.2
		O	679	473	166	0.1	0.2
	D2	A	711	316	307	0.5	0.3
		O	628	326	218	0.6	0.2
2013	UD1	A	934	427	440	0.2	
		O	983	406	496	0.6	
	UD2	A	1171	466	604	0.8	
		O	1017	414	509	0.8	
	R1	A	1228	438	631	0.2	
		O	1264	387	725	0.3	
	R2	A	921	382	363	0.4	
		O	839	349	364	0.2	
	D1	A	503	792	-176	0.1	
		O	642	559	124	0.0	
	D2	A	852	352	377	0.1	
		O	980	390	474	0.0	

Table 4. Global warming potential (GWP) of different land uses (UD = undrained, R = restored, D = drained) based on gas fluxes calculated for growing seasons 2011 and 2013. GWP calculated based on 100-year time horizon (Myhre et al. 2013). The values are expressed as g $CO_{2\text{-eq}}$ m^{-2} $season^{-1}$ and positive values indicate net warming impact to atmosphere. The estimates for drained sites include the annual above-ground tree stand CO_2 sequestration, which would occur mostly during the growing season.

Study site	GWP_2011	GWP_2013
UD1	156	462
UD2	-114	145
R1	243	516
R2	-137	240
D1	178	334
D2	709	971

Figures

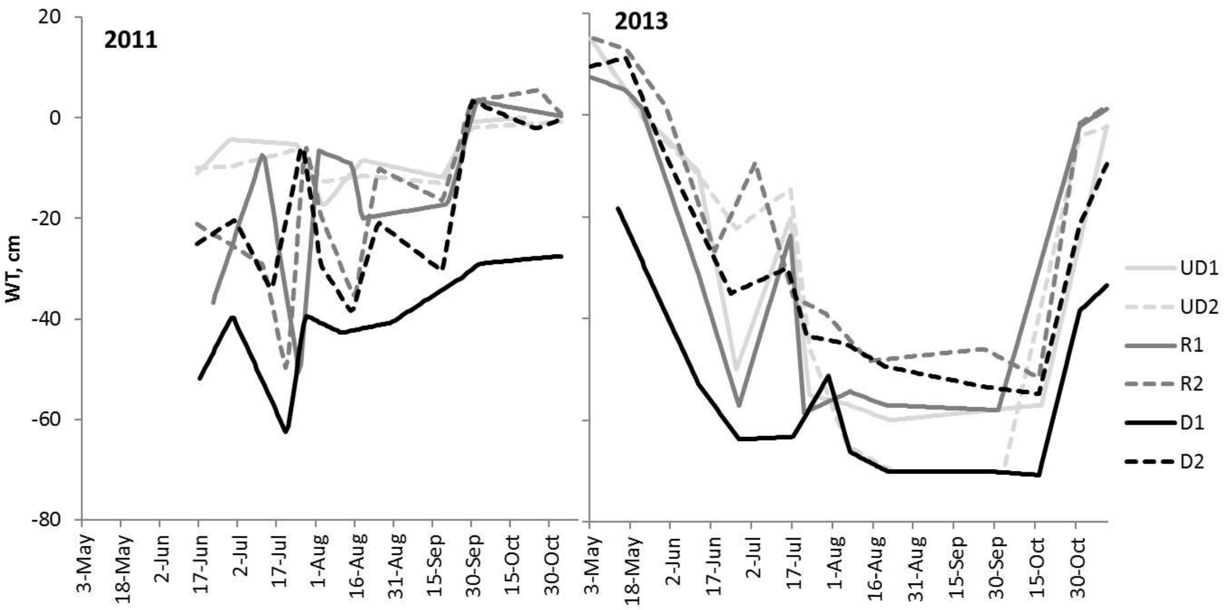

Figure 1. Water table (WT) in years 2011 and 2013 in the six study sites. UD = undrained, R = restored and D= drained. Values below zero indicate WT below soil surface.

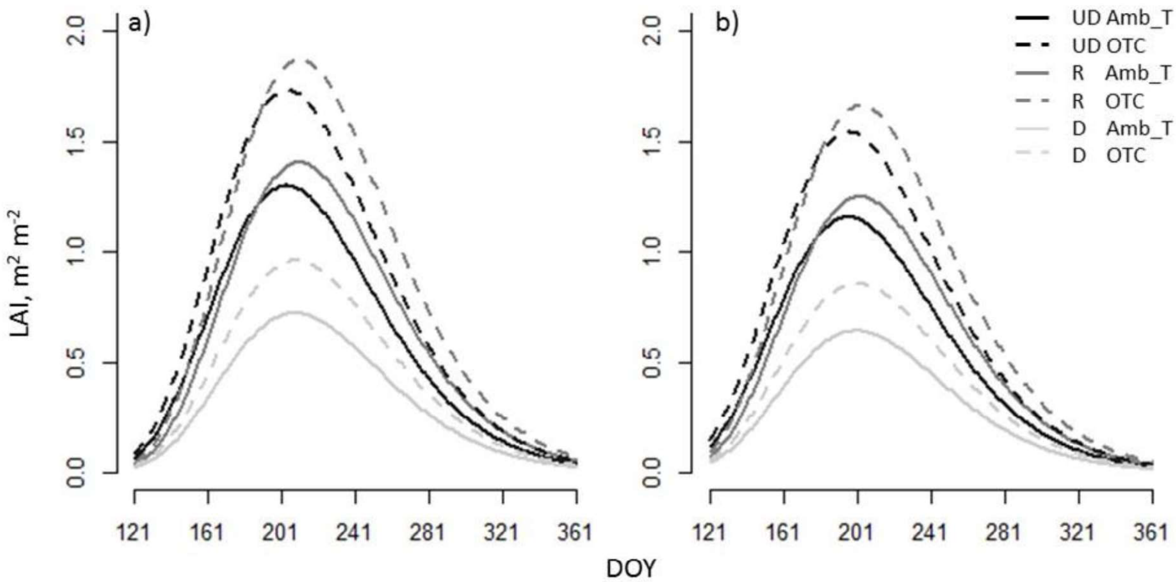

Figure 2. Seasonal development (May to December) of leaf area index (LAI) during a) year 2011 and b) year 2013, in ambient-T (Amb_T, solid lines) and OTC warmed plots (dashed lines) at undrained (UD), restored (R) and drained (D) sites belonging to Group 1. As LAI of group 2 behaved at similar manner to group 1, those results are not shown here.

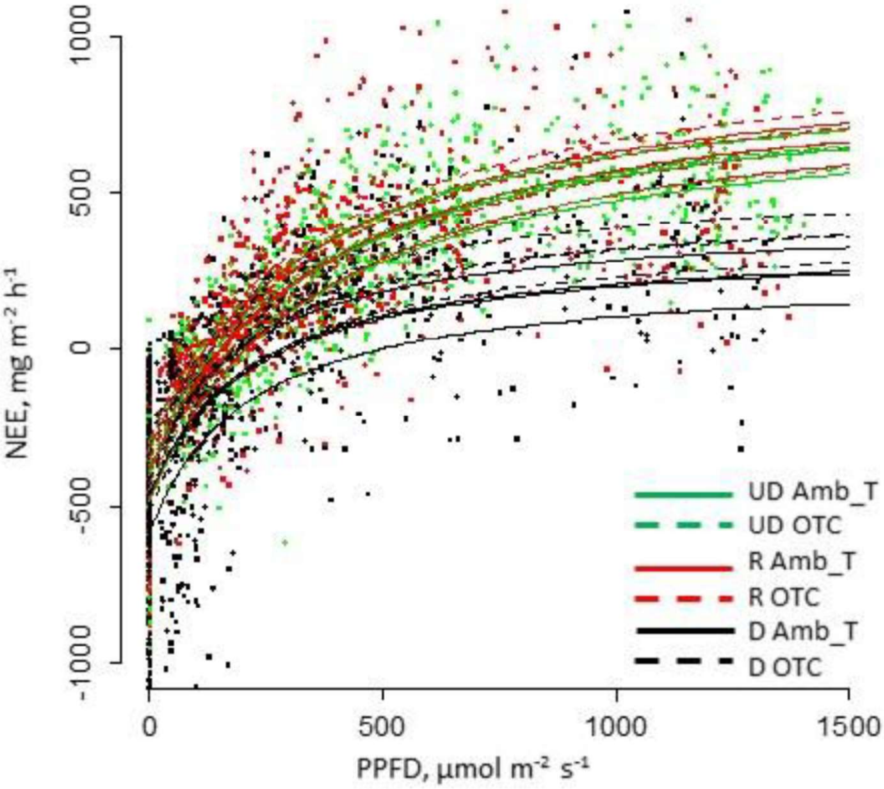

Figure 3. Light response of net ecosystem CO_2 exchange (NEE) under different land use and warming treatments. Scatter plot shows the measured fluxes, while the different response curves are based on CO_2 model and represent the three land uses (UD = undrained, R = restored, D = drained), warming treatments (Amb_T = ambient-T, OTC = OTC warming), measurement years (2011, 2013) and site groups 1 and 2. Therefore, the four lines per land use x warming treatment describe the variability caused by year and site group.

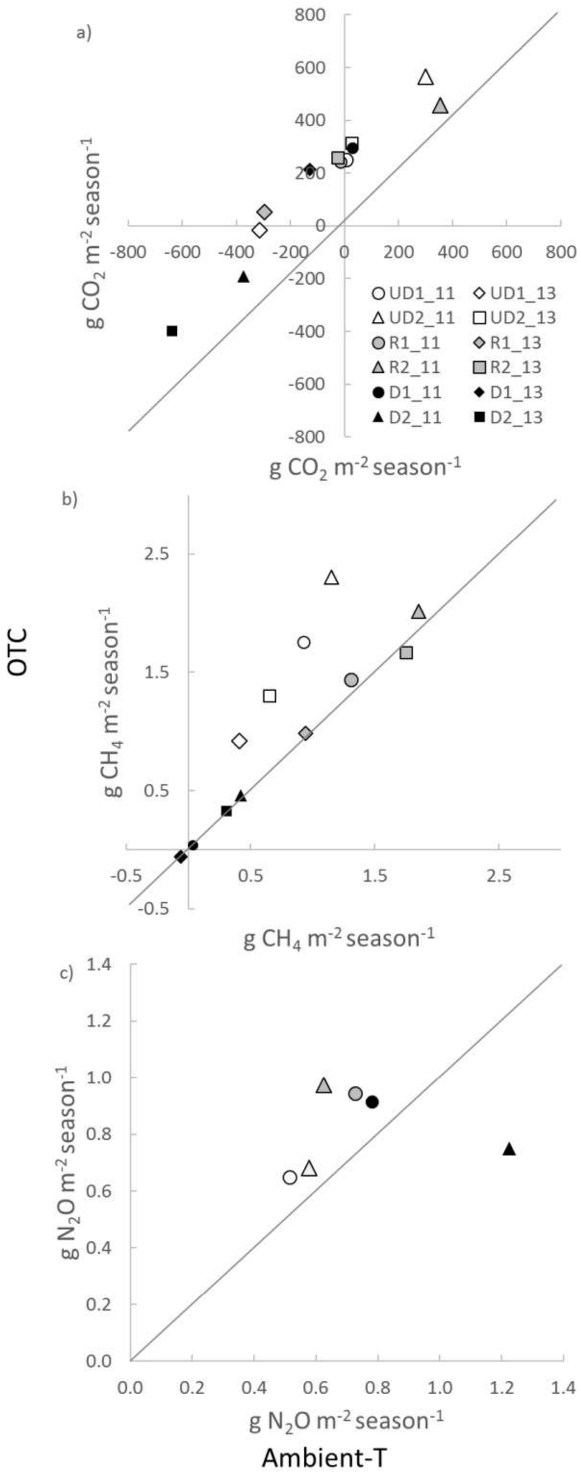

Figure 4. Scatterplot of Ambient-T vs. OTC-warmed seasonal (May-September) cumulative flux of a) net ecosystem CO_2 exchange (NEE), b) methane, c) nitrous oxide. Seasonal fluxes are calculated for OTC-warmed and ambient-T plots for each study site and for seasons 2011 and 2013. UD: undrained, R: restored, D: drained. We added the annual average tree stand carbon sequestration of 959 and 423 g CO_2 m^{-2} to the field layer NEE estimates of sites D1 and D2, respectively. 1:1 line is shown for each GHG component.

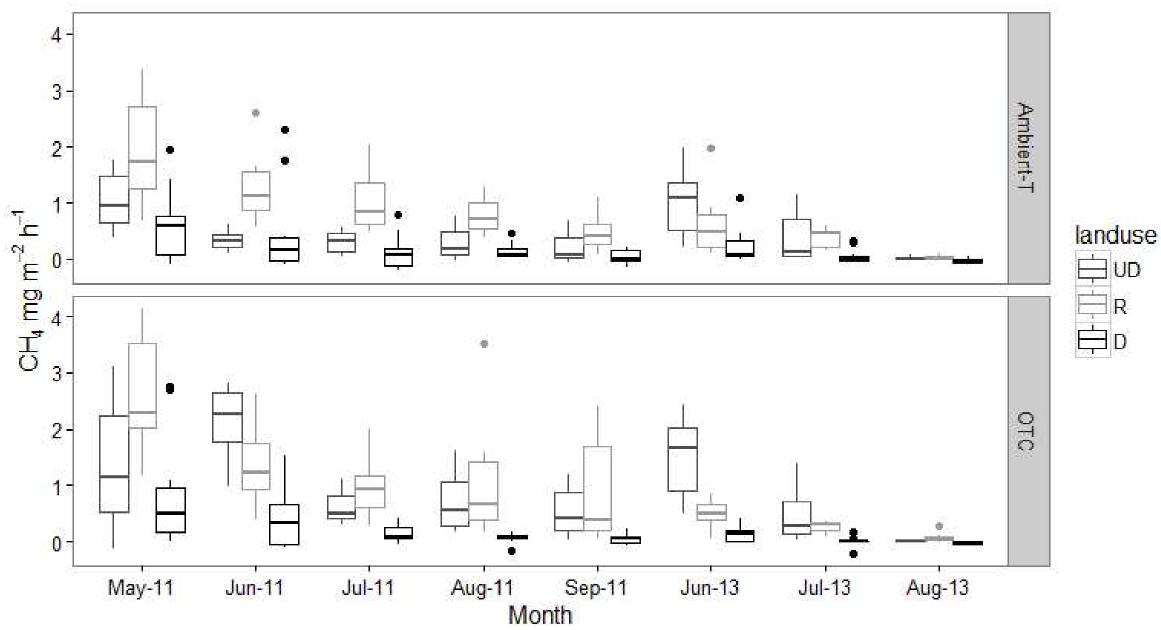

Figure 5. Box-plot of average measured CH_4 fluxes at undrained (UD), restored (R) and drained (D) sites under warmed (OTC) or ambient-T (C) temperature during the eight measurement campaigns at May, June, July, August and September of year 2011 and June, July and August of year 2013. Boxes represent range of middle two quartiles of the data, horizontal line is the median, and whiskers show the range excluding outliers (points).

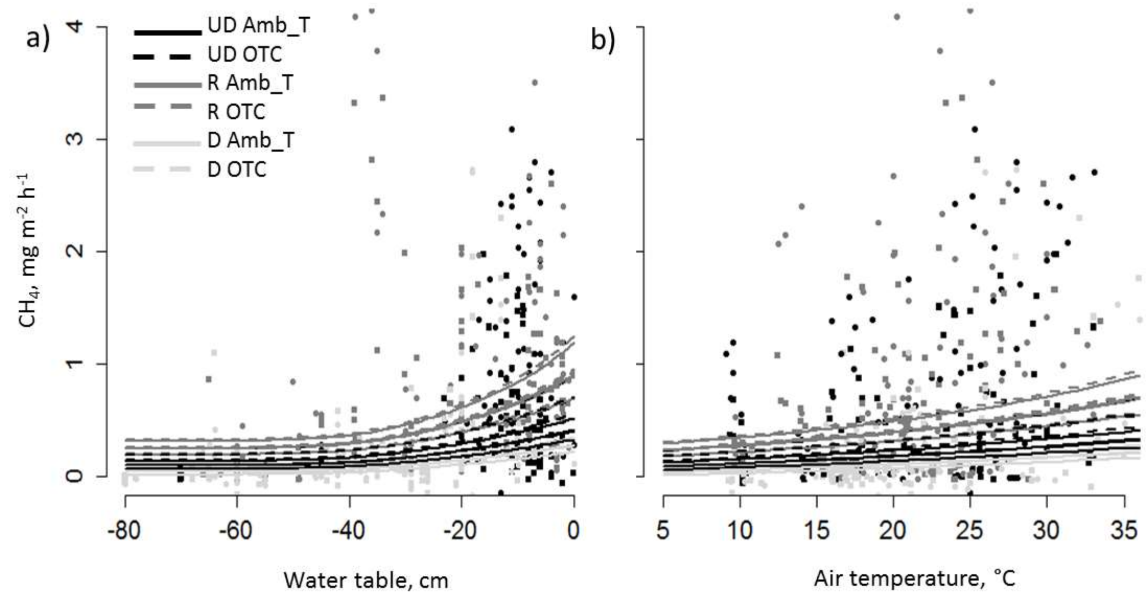

Figure 6. Scatter plot of measured fluxes and response curves from full CH_4 model (Appendix 3). a) CH_4 flux related to water table level and b) to air temperature. Environmental variables are standardized to following values based on data averages: WT: -26.5 cm, Ta: 20.79°C, T5: 13.01 °C, field-layer LAI: 1.08 m^{2}m^2.

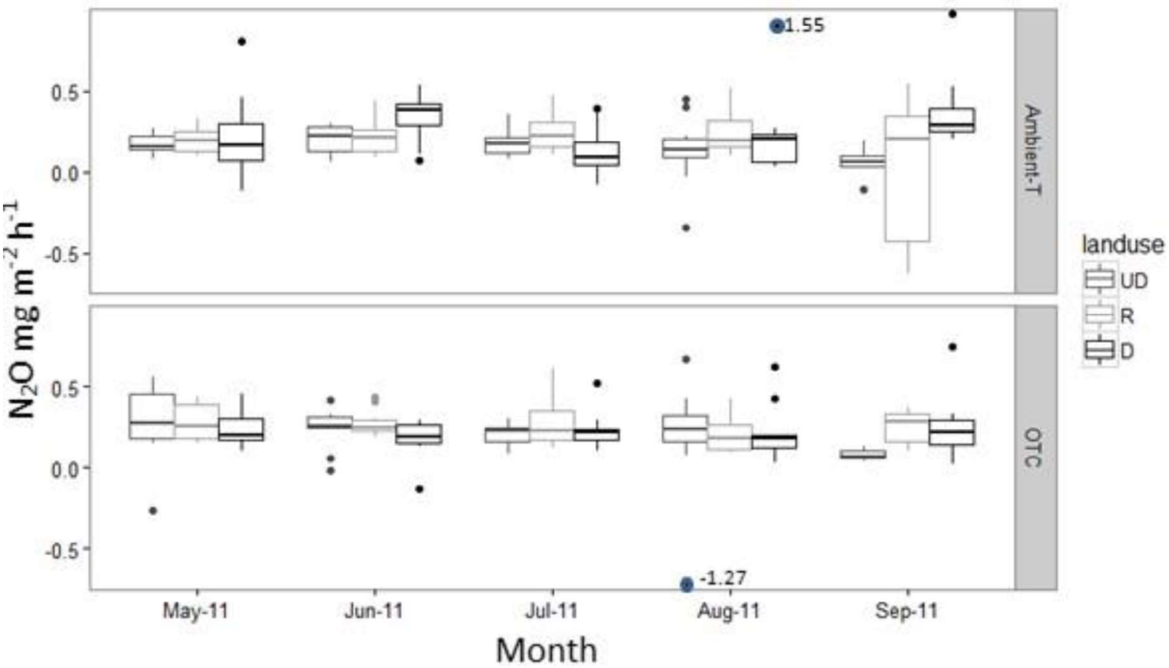

Figure 7. Box-plot of N_2O fluxes at undrained (UD), restored (R) and drained (D) sites under warmed (OTC) or ambient-T (C) temperature during the five measurement campaigns at May, June, July, August and September of year 2011. At the boxplot, the line that divides the box into two parts represents the median of the data and the end of the box shows the upper and lower quartiles. The whickers show the highest and lowest value excluding outliers, which are represented by points. The two extreme outliers are shown with respective values.

Supporting information for online publication **Nonlinear mixed-effect models for leaf area index** and GHG fluxes

Laine et al. Impacts of drainage, restoration and warming on boreal wetland greenhouse gas fluxes

0000-0003-2989-1591

Supporting information 1. Nonlinear mixed-effect model based on leaf area index

Supporting information 2. Nonlinear mixed-effect model based on CO_2 flux measurements

Supporting information 3. Linear mixed effect models based on CH_4 measurements

Supporting information 4. Linear mixed effect models based on N_2O measurements

Supporting information 1. Nonlinear mixed-effect model based on leaf area index

Table S1.1. ANOVA results of the non-linear mixed effects models (Eq. 1-3) for the differences in leaf area index (LAI) between land use (undrained, drained, restored), warming treatment, years (2011 and 2013) and group (two groups of sites: UD1, R1 and D1, and UD2, R2 and D2). LMAX is maximum LAI during growing season and DMAX is the day of year when maximum is reached.

Source	numDF	denDF	LMAX F-value	p-value	DMAX F-value	p-value
Year	1	648	8.12	0.005	19.93	<.0001
Land use	2	648	6.7	0.001	5.08	0.006
Warming	1	648	8.64	0.003	0.06	0.803
Group	1	648	1.69	0.194	12.32	0.001

Table S1.2. Parameter estimates and random effects of nonlinear mixed-effects model of leaf area index (LAI) model (Eq.1-3). The bolded values are significant at $p<0.05$. Then drained site of group 1 with no warming in year 2011 is used as control.

Source	DF	ln(LMAX) Value	Std.Error	ln(DMAX) Value	Std.Error	ln(G) Value	Std Error
Fixed part							
Intercept	648	0.26	0.17	5.32	0.01	-1.52	0.121
Year 2013	648	**-0.12**	0.04	**-0.04**	0.01		
Restoration	648	0.08	0.20	**0.03**	0.01		
Drainage	648	**-0.59**	0.20	0.02	0.01		
Warming	648	**0.29**	0.10	0.002	0.01		
Group2	648	0.21	0.16	**-0.03**	0.01		
Random effects and residual							
var(a_i)		0.16^2		0		0.29^2	
var(b_{ij})		0.34^2		0.01^2		0	
var(c_{ijk})		0.18^2		0.03^2		0.08^2	
var(ε_{ijkl})		0.25^2					

Supporting information 2. Nonlinear mixed-effect model based on CO_2 flux measurements

Table S2.1. ANOVA results of the simple non-linear mixed effects models, including only categorical treatments, based on CO_2 measurements (Eq. 4-7).

		numDF	denDF	F-value	p-value
ln(PMAX)	Intercept				
	Year	1	2241	0.03	0.854
	Land use	4	2241	13.46	<.0001
	Warming	3	2241	0.72	0.538
	Group	1	2241	0.19	0.667
	Land use :Warming	2	2241	0.88	0.415
ln(R)	Intercept				
	Year	1	2241	42.75	<.0001
	Land use	4	2241	0.99	0.409
	Warming	3	2241	1.39	0.244
	Group	1	2241	8.15	0.004
	Land use :Warming	2	2241	0.03	0.970
ln(α)	Intercept				
	Land use	2	2241	13.85	<.0001

Table S2.2. Parameter estimates and random effects of the simple nonlinear mixed effect model, including only categorical treatments, based on CO_2 measurements (Eq. 4-7). The undrained site of group 1 with no warming in year 2011 is used as control.

Fixed part		Value	Std.Error	DF	t-value	p-value
ln(PMAX)	Intercept	7.15	0.06			
	Year2013	0.01	0.03	2241	0.18	0.854
	Restored	0.03	0.07	2241	0.42	0.671
	Drained	-0.43	0.08	2241	-5.68	<.0001
	Warming	-0.02	0.06	2241	-0.36	0.717
	Group2	-0.02	0.04	2241	-0.43	0.667
	Restored : Warming	0.03	0.08	2241	0.36	0.721
	Drained : Warming	0.11	0.09	2241	1.29	0.199
ln(R)	Intercept	6.00	0.10			
	Year2013	0.19	0.03	2241	6.54	<.0001
	Restored	-0.02	0.12	2241	-0.20	0.845
	Drained	0.18	0.12	2241	1.47	0.142
	Warming	-0.08	0.09	2241	-0.96	0.336
	Group2	-0.22	0.08	2241	-2.85	0.004
	Restored : Warming	-0.02	0.12	2241	-0.13	0.899
	Drained : Warming	-0.03	0.12	2241	-0.25	0.804
ln(α)	Intercept)	5.82	0.07			
	Restored	0.08	0.10	2241	0.81	0.420
	Drained	-0.48	0.11	2241	-4.30	<.0001
Random part		**PMAX**	**R**	**α**		
var(a_i)		0.00^2	0.09^2	0.06^2		
var(b_{ij})		0.00^2	0.16^2	0.00^2		
var(c_{ijk})		0.19^2	0.11^2	5.42^2		
var(d_{ijkl})		0.25^2	0.37^2	0		
corr(d_{ijkl}^P,d_{ijkl})		1				
var(ε_{ijklm})		100.25^2				

Table S2.3. ANOVA results of the full nonlinear mixed effect model, including environmental variables, based on CO_2 measurements (Eq. 4-7). Ta= air temperature, a1 = spline component based on a three-knot spline, LAI2 = is the plot level modelled leaf area (Eq 1-3) transformed as ln(1-exp(-LAI)), min(t15, 10) = soil temperature at 15 cm depth, log(LAI) = is logarithmically transformed LAI.

		numDF	denDF	F-value	p-value
ln(PMAX)					
	Year	1	2235	19.77	<.0001
	Land use	4	2235	1.63	0.163
	Warming	3	2235	1.08	0.355
	Group	1	2235	5.58	0.018
	Ta/a1	2	2235	19.87	<.0001
	LAI2	1	2235	219.32	<.0001
	Land use :Warming	2	2235	0.40	0.669
ln(R)					
	Year	1	2235	188.08	<.0001
	Land use	4	2235	1.31	0.262
	Warming	3	2235	4.42	0.004
	Group	1	2235	3.88	0.048
	Ta	1	2235	365.16	<.0001
	Log(LAI)	1	2235	95.89	<.0001
	min(T15, 10)	1	2235	220.53	<.0001
	Land use : Warming	2	2235	0.40	0.670
ln(α)					
	Land use	2	2235	7.72	0.001

Table S2.4. Parameter estimates and random effects of the full nonlinear mixed effect model, including environmental variables, based on CO_2 measurements (Eq. 4-7). The undrained site of group 1 with no warming in year 2011 is used as the control.

Fixed part		Value	Std.Error	DF	t-value	p-value
ln(PMAX)	Intercept	6.88	0.13			
	Year2013	0.15	0.03	2235	4.45	<.0001
	Restored	-0.01	0.11	2235	-0.05	0.961
	Drained	-0.16	0.11	2235	-1.43	0.152
	Warming	-0.08	0.08	2235	-0.95	0.343
	Group2	-0.15	0.06	2235	-2.36	0.018
	Ta	0.03	0.01	2235	6.29	<.0001
	a1	0.00	0.00	2235	-5.68	<.0001
	LAI2	0.65	0.04	2235	14.81	<.0001
	Restored :Warming	0.05	0.11	2235	0.47	0.641
	Drained : Warming	-0.05	0.12	2235	-0.44	0.663
ln(R)	Intercept	4.02	0.18			
	Year2013	0.28	0.02	2235	13.71	<.0001
	Restored	-0.06	0.22	2235	-0.27	0.789
	Drained	0.39	0.22	2235	1.82	0.069
	Warming	-0.14	0.09	2235	-1.61	0.106
	Group2	-0.17	0.09	2235	-1.97	0.049
	Ta	0.03	0.00	2235	19.11	<.0001
	Log(LAI)	0.24	0.02	2235	9.79	<.0001
	Pmin(T15,10)	0.14	0.01	2235	14.85	<.0001
	Restored: Warming	-0.01	0.12	2235	-0.08	0.935
	Drained: Warming	-0.10	0.12	2235	-0.81	0.418
ln(α)	Intercept	5.65	0.09			
	Restored	0.14	0.13	2235	1.14	0.254
	Drained	-0.38	0.13	2235	-2.80	0.005
Random part		PMAX	R	α		
var(a_i)		0.06^2	0.20^2	0.1^2		
var(b_{ij})		0.13^2	0.18^2	0.00^2		
var(c_{ijk})		0.17^2	0.04^2	0.25^2		
var(d_{ijkl})		0.23^2	0.19^2			
corr(d_{ijkl}^P,d_{ijkl})			0.58^2			
var(ε_{ijklm})			78.41			

Supporting information 3. Linear mixed effect models based on CH_4 measurements

Table S3.1. ANOVA results of the simple linear mixed effect model, including categorical treatments, based on CH_4 measurements, using the transformation $-1/(CH_4 + 0.4)$.

	Sum Sq	mean Sq	NumDF	DenDF	F.value	Pr(>F)
Year	0.66	0.66	1	6.02	2.43	0.170
Land use	2.29	1.14	4	2.48	3.78	0.182
Warming	1.15	1.15	3	51.86	3.65	0.018
Group	0.27	0.27	1	0.00	0.98	
Land use:Warming	1.86	0.93	2	51.84	3.39	0.041

Table S3.2. Parameter estimates and random effects of the simple linear mixed effect model, including categorical treatments, based on CH_4 measurements. Measurements from the undrained site of group 1 with no warming in year 2011 are used as the control.

Fixed part	Estimate	Std.Error	df	t	p value
Intercept	-1.49	0.36			
Year 2013	-0.50	0.32	6.0	-1.56	0.170
Restored	0.40	0.38	2.2	1.06	0.395
Drained	-0.61	0.38	2.2	-1.62	0.237
Warming	0.35	0.11	51.7	3.30	0.002
Group2	0.30	0.30	2.0	0.99	0.427
Restored : Warming	-0.33	0.15	52.7	-2.18	0.034
Drained : Warming	-0.35	0.15	50.9	-2.32	0.024
Random part	**Variance**				
site	0.36^2				
plot:site	0.15^2				
mestime	0.43^2				
Residual	0.52^2				

Table S3.3. ANOVA results of the full linear mixed effect model, including environmental variables, for CH_4 measurements ($-1/CH_4+0.4$). LAI_S = is the modelled plot level leaf area including only sedges (Eq 1-3), WT = water table, a1 = the second term of the three-knot spline for WT, Ta= air temperature, T5 = soil temperature in 5 cm depth.

	Sum Sq	mean Sq	NumDF	DenDF	F.value	Pr(>F)
Year	0.06	0.06	1	7	0.247	0.635
Land use	1.04	0.52	4	2.7	3.224	0.195
Warming	0.83	0.83	3	51	3.923	0.013
Group	0.06	0.06	1	2	0.257	0.662
LAI_S	0.62	0.62	1	229	2.494	0.116
WT and a1	0.05	0.05	2	410	12.158	<.0001
Ta	1.56	1.56	1	373	6.234	0.013
T5	0.18	0.18	1	432	0.704	0.402
Land use:Warming	1.43	0.71	2	50	2.859	0.067

Table S3.4. Parameter estimates and random effects of the full linear mixed effect model including environmental variables, based on CH_4 measurements. Measurements from undrained site of group 1 with no warming in year 2011 are used as the control.

Fixed part	Estimate	Std.Error	df	t	p value
Intercept	-2.55	0.54			
Year2013	-0.13	0.27	7	-0.50	0.635
Restored	0.46	0.36	2	1.28	0.320
Drained	-0.25	0.36	2	-0.68	0.558
Warming	0.32	0.11	52	2.97	0.005
Group2	0.15	0.29	2	0.51	0.662
LAI_S	0.11	0.07	230	1.58	0.116
WT	0.00	0.01	404	0.45	0.653
a1	0.00	0.00	416	1.83	0.069
Ta	0.02	0.01	373	2.50	0.013
T5	0.02	0.02	432	0.84	0.402
Restored: Warming	-0.30	0.15	52	-1.95	0.057
Drained: Warming	-0.33	0.15	49	-2.18	0.034
Random part	**Variance**	.			
site	0.34^2				
plot:site	0.16^2				
mestime	0.34^2				
Residual	0.50^2				

Supporting information 4. Linear mixed effect models based on N_2O measurements

Table AS.1. ANOVA results of the simple linear mixed effect model, including only categorical treatments, for N_2O measurements.

	Sum Sq	mean Sq	NumDF	DenDF	F.value	Pr(>F)
Land use	0.17	0.09	4	284.12	2.74	0.029
Warming	0.11	0.11	3	284.12	2.96	0.033
group	0.02	0.02	1	284.33	0.56	0.455
Land use:Warming	0.14	0.07	2	284.14	2.46	0.087

Table S4.2. Parameter estimates and random effects of the simple linear mixed effect model, including only categorical treatments, based on N_2O measurements. Measurements from undrained site of group 1 with no warming in year 2011 are used as the control.

Fixed part	Estimate	Std.Error	df	t	p value
Intercept	0.14	0.03			
Restored	0.04	0.03	284.11	1.03	0.302
Drained	0.10	0.03	284.19	2.90	0.004
Warming	0.06	0.03	284.11	1.80	0.073
group2	0.01	0.02	284.33	0.75	0.455
Restored :Warming	0.02	0.05	284.08	0.32	0.751
Drained :Warming	-0.08	0.05	284.21	-1.74	0.084
Random part	**Variance**				
site	0				
plot:site	0				
meastime	0.02^2				
Residual	0.17^2				

Table S4.3. ANOVA results of the full linear mixed effect model including also environmental variables for log transformed N_2O measurements. WT = water table, Ta= air temperature and LAI = is the modelled plot level leaf area (Eq 1-3),

	Sum Sq	mean Sq	NumDF	DenDF	F.value	Pr(>F)
Land use	0.100	0.050	4	285	2.07	0.084
Warming	0.086	0.086	3	285	2.53	0.058
Group	0.020	0.020	1	285	0.68	0.409
WT	0.012	0.012	1	285	0.41	0.525
Ta	0.052	0.052	1	285	1.82	0.178
LAI	0.017	0.017	1	285	0.61	0.437

Table S4.4. Parameter estimates and random effects of the full linear mixed effect model including environmental variables, based on log transformed N_2O measurements. Measurements from undrained site of group 1 with no warming in year 2011 are used as the control.

Fixed part	Estimate	Std.Error	df	t	p value
Intercept	0.085	0.040			
Restored	0.033	0.034	285	0.97	0.333
Drained	0.094	0.040	285	2.33	0.020
Warming	0.061	0.035	285	1.73	0.084
Group2	0.018	0.021	285	0.83	0.409
WT	-0.001	0.001	285	-0.64	0.525
Ta	0.002	0.001	285	1.35	0.178
LAI	0.012	0.015	285	0.78	0.437
Restored :Warming	0.011	0.048	285	0.22	0.828
Drained :Warming	-0.085	0.049	285	-1.76	0.080
Random part	**Variance**				
site	1.74E-08^2				
plot:site	0.00E+00^2				
meastime	0.00E+00^2				
Residual	1.69E-01^2				